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Shrimp equalize marginal payoffs in an evolutionary game with condition dependence

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ABSTRACT

Sex-changing shrimp support the marginal value rule from evolutionary game theory in their facultative adjustment of sex ratio.

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In a typical evolutionary game where the fitness payoffs to players of each of two tactics (*A* or *B*) are frequency dependent, the evolutionary equilibrium (ESS; Maynard Smith, 1982) equalizes the average fitness of *A* and *B*; this concept of a 'mixed ESS' has proven very useful (Gross, 1996; Brockmann, 2001). A slightly more complicated game is where there are again two tactics (*A* and *B*) and some phenotypic condition variable such as body size. Fitness depends upon size *and* the frequency of *A* and *B* such that the ESS rule at evolutionary equilibrium is of the form, *if small play A*, *if large play B*. Since, by assumption, the size distribution itself is not altered by the decision to play *A* or play *B*, the proportion playing *A* or *B* is adjusted only by adjusting the *threshold size* (τ) (*condition*) *for changing from A to B*, as illustrated in Fig. 1.

The ESS rule to find τ is that the fitness payoff to an individual *of size* τ should be the same regardless of whether the individual plays *A* or *B* (Charnov *et al.*, 1978; West-Eberhard, 1979; Charnov, 1982, 1993; Parker, 1982; Repka and Gross, 1995; Gross, 1996): condition-dependent decisions yield a new rule to find the ESS mixture of *A* and *B* – **equalize the marginal fitness payoff for *A* and *B***. Whereas a mixed ESS equalizes the average fitness of *A* and *B*, the condition-dependent ESS mixture implies the equalization of *A* and *B* fitness at the margin, the change-over condition τ. While there is much field evidence for both frequency dependence *and* condition dependence of fitness (e.g. Gross, 1996; Brockmann, 2001), I have found no examples that really test the equalization of marginal fitness.

The last statement is not quite true, since some sex-allocation cases (Charnov, 1982) imply equalization of marginal fitness over the conditional decision to be (to produce) males (*A*) versus females (*B*). Let me point out one particularly elegant example from sex-changing

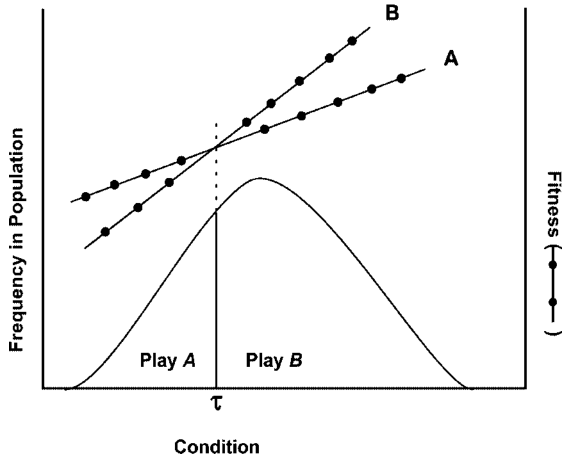

Fig. 1. A condition-dependent ESS mixture. Individuals in poor condition play *A*, while those in better condition play *B*. The switch point (τ) equalizes the fitness of *A* versus *B at that point* (after Charnov, 1993; Gross, 1996).

Pandalid shrimp. Off the US west coast, the commercially important shrimp, *Pandalus jordani*, breeds each fall and has two breeding age groups (Charnov and Hannah, 2002); first breeders are about half the body mass of second breeders. In most years, all second breeders are female, while first breeders can be either sex. Fecundity is size dependent, with a second breeder having W (2–3) times the eggs of a female first breeder. Charnov *et al.* (1978) showed that, provided growth and mortality (to second breederhood) are independent of first breeder choice of sex, the ESS proportion of females among the first breeders should equal

$$\frac{1}{2}\left[1 - W\left(\frac{1-P}{P}\right)\right] \tag{1}$$

where P is the proportion of the breeding population that are first breeders. Of course, this result must be non-negative, so it can only hold for appropriate P and W (Charnov and Hannah, 2002).

Equation (1) can be derived in several ways, but let me now show how it follows from equalization of marginal fitness over the choice of male or female among the first breeders. Let there be two sizes of shrimp (big, small) and let P be the proportion of the breeding population of size N that are small. Let all big shrimp choose to be female; each big female will produce F_2 eggs, while each small female will produce F_1 eggs. If r is the proportion of small shrimp that choose to be male, the ESS r is where a *small shrimp produces* (female) *or fertilizes* (male) *the same number of eggs*. This equalizes male versus female fitness for a small shrimp (Charnov *et al.*, 1978). Now, female fitness of a small shrimp is F_1, whereas male fitness of a small shrimp is:

$$\left(\frac{1}{\text{number of males}}\right) \times (\text{eggs produced by all females}) = \frac{1}{N \cdot P \cdot r} \times [N \cdot P(1-r)F_1 + N(1-P)F_2]$$

The ESS r equalizes these two small shrimp fitnesses, or:

$$F_1 = \left(\frac{1}{N \cdot P \cdot r}\right)(N \cdot P(1-r)F_1 + N(1-P)F_2) \tag{2}$$

Set $W = F_2/F_1$, then equation (2) can be rewritten as:

$$r = 1 - r + \left(\frac{1-P}{P}\right)W$$

$$1 - 2 \cdot r = -\frac{(1-P)}{P}W$$

$$2(1-r) = 1 - \frac{(1-P)}{P}W$$

$$1 - r = \frac{1}{2}\left[1 - \frac{(1-P)}{P}W\right]$$

which is equation (1).

The beauty of the example is its transparent simplicity. The female proportion of first breeders $(1 - r)$ has been shown in field data (by correlation analysis) to track year-to-year changes in age structure, the proportion of first breeders (P); variation in P is caused mainly by variation in recruitment to the first-breeding age group (small), and the first breeders adjust r accordingly (Charnov *et al.*, 1978; Charnov and Hannah, 2002). The equalization of male versus female fitness at the age/size of sex change has long been used in sex-change theory to predict things like the ESS breeding sex ratio (e.g. Charnov, 1982, p. 140; Charnov and Bull, 1989; Charnov, 1993, Ch. 3). Indeed, Charnov *et al.* (1978) originally claimed that equation (1) meant that the fitness of a first-breeder male was equal to the fitness of a first-breeder female (last sentence, p. 204); as strongly noted by Brockmann (2001), sex allocation provides some of the finest examples of frequency dependence mixed with condition dependence of fitness.

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